# A new species of Santinezia (Opiliones: Cranaidae) from Panama 

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#### Abstract

A new species, Santinezia noctiscansor, most similar to members of the $S$. festae group, is described from central Panama; this species is the only member of the genus that occurs in Central America. Our examinations of adults and nymphs collected from Coclé and Panamá Provinces revealed that males are sexually mature as penultimate nymphs. The subadult strongly resembles the adult with respect to coloration, scutal outline, armature of femora III-IV, and penis morphology, but differs in having fewer tarsomeres on each leg, a smaller body size (scutal length and width), and a much smaller tubercle on the ventral surface of coxa IV. Natural history observations are provided for specimens collected from the field site in Coclé Province.


Keywords: Harvestman, Laniatores, natural history, Neotropics

In the catalogue of the Laniatores of the New World, Kury (2003) listed only three species of cranaids (all members of the subfamily Cranainae) occurring in Central America: Comboyus alblineatus Roewer 1943 and Phareicranaus magnus (Roewer 1932) from Panama, and P. ornatus Roewer 1932 from Costa Rica and Panama. In Pinto-da-Rocha \& Kury (2003), P. magnus was transferred to Neocranaus. In a brief review of the geographic distribution of the Cranaidae, Pinto-da-Rocha \& Kury (2007) stated, but did not specify, that only two species in the family occur in Central America (Panama and Costa Rica). Given that C. albilineatus was not examined by Pinto-da-Rocha \& Kury (2003), it seems likely that this species was overlooked in the later review.
In this study, we describe Santinezia noctiscansor based upon examinations of adult and subadult specimens collected from two sites in Panama. The genus Santinezia consists of 21 species of medium to large harvestmen (scutal length: $6-16 \mathrm{~mm}$ ) that occur primarily in northern South America (Pinto-da-Rocha \& Kury 2003, 2007). Males possess a large tubercle on the ventral surface of coxa IV, a feature that represents the most reliable character used for distinguishing between members of the genera Santinezia and Phareicranaus (Pinto-da-Rocha \& Kury 2003). In comparison to adult females, cranaid males have more pronounced armature on leg IV (especially the femur, but also the tibia in several species) and somewhat enlarged chelicerae (Pinto-da-Rocha \& Kury 2007). During postembryonic development, the sexually dimorphic femur IV is observable in the antepenultimate nymph (Townsend et al. 2009). Presently, three species groups (curvipes, festae, and gigantea) are distinguished on the bases of the armature on femur IV and tibia IV, the position of the ventral tubercle on coxa IV, and penis morphology (Pinto-da-Rocha \& Kury 2003). Little is known about the natural history of these harvestmen. On the Caribbean island of Trinidad, adult
S. serratotibialis (a member of the curvipes group) climb vegetation after dusk (Townsend et al. 2008a), occupy diurnal shelters within rotting logs and palm frond sheaths (Townsend et al. 2008a), exhibit parental care through the guarding of eggs (Machado \& Warfel 2006) and nymphs (Townsend et al. 2009), and are infrequently parasitized by larval erythraeid mites (Townsend et al. 2008b).

## METHODS

The adult male holotype and subadult male paratype of Santinezia noctiscansor were collected from montane rainforests in Coclé Province near the village of El Cope and are deposited in the American Museum of Natural History (AMNH). We examined an adult male paratype and three subadult paratypes of $S$. noctiscansor from the collections of the Museo de Invertebrados G.B. Fairchild (MIUP) at the Universidad de Panama. All specimens were observed and photographed in $70 \%$ ethanol with a digital Leica EZ 4D stereomicroscope. We took measurements with the aid of an image capturing system.

Because the taxonomic literature for the Laniatores is rich with potentially ambiguous terms for macroscopic cuticular structures (e.g., spines, tubercles, and apophyses), collectively referred to as "macrosculpture" (Acosta et al. 2007), we employed the terminology suggested by Acosta et al. (2007) with regard to spines (structures that insert into sockets) and tubercles (small, blunt projections that may or may not bear setae). However, we refer to larger structures as "spiniform tubercles" rather than "apophyses" (Acosta et al. 2007) or "spines" (e.g., Goodnight \& Goodnight 1947).

For comparative purposes, we examined the female holotype of Phareicranuas ornatus Roewer 1932 (RII/ 25971 68-42) from Senckenberg Museum, Frankfurt, Germany (SMF) as well as multiple adult and nymphal specimens of Santinezia serratotibialis Roewer 1932 from AMNH.

## KEY TO THE CRANAIDAE OF CENTRAL AMERICA

1. Only second free tergite with a pair of median tubercles; sulci I-II with conspicuous white stripes; femur IV of male armed with a large basal pair of spiniform tubercles; tarsus II with 28 segments . . . . . . . . . . . Comboyus albilineatus Roewer 1943 (Panama) Second and third free tergites with a median pair of tubercles; sulci I-II without conspicuous stripes; femur IV of male not armed with large, basal, spiniform tubercles on the prolateral and retrolateral surfaces; tarsus II with less than 20 segments
2. Coxa IV of male armed ventrally with large, median tubercle tarsus I with 9 segments Santinezia noctiscansor new species (Panama)
Coxa IV of male ventrally unarmed; tarsus I with less than 9 tarsomeres
3. Leg II greater than 50 mm ; tarsal formula 8:17:7:7 (Roewer 1932) or 7:11-12:7:7 (Pinto-daRocha and Kury 2003)

Leg II less than 50 mm ; tarsal formula 8:13-14:9:10 Neocranaus magnus (Roewer 1932) (Panama) Phareicranaus ornatus Roewer 1932 (Costa Rica)

## SYSTEMATICS

## Family Cranaidae Roewer 1913 <br> Santinezia Roewer 1923

Inezia Roewer 1913:392 (preoccupied by Inezia Cherrie 1909); Mello-Leitão 1926:39; Mello-Leitão 1932:113 (type species Inezia gigantea Roewer 1913, by monotypy).
Santinezia Roewer 1923:553 (replacement name); MelloLeitão 1932:122; Roewer 1932:289; Mello-Leitão 1935:96; Kästner 1937:389; Soares \& Soares 1948:616; Roewer 1963:69; González-Sponga 1989:59 (type species Inezia gigantea Roewer 1913); Pinto-da-Rocha \& Kury 2003:181; Kury 2003:97.
Niebla Roewer 1925:27; Roewer 1932:348; Soares \& Soares 1948:610 (type species Niebla festae Roewer 1925, by monotypy); Synonymy established by Pinto-da-Rocha \& Kury 2003:181.
Chondrocranaus Roewer 1932:341; Soares \& Soares 1948:592 (type species Chondrocranaus scriptus Roewer 1932, by monotypy). Synonymy established by Pinto-da-Rocha \& Kury 2003:181.
Macuchichola Mello-Leitão 1943:4; Soares \& Soares 1948:606 (type species Macuchicola arthrocentrica Mello-Leitão 1943, by original designation. Synonymy established by Pinto-daRocha \& Kury 2003:181.
Carvalholeptes H. Soares 1970:330 (type species Carvalholeptes singularis H. Soares 1970, by original designation). Synonymy established by Pinto-da-Rocha \& Kury 2003:181.

## Santinezia noctiscansor new species

(Figs. 1-7)
Type material.-PANAMA: Coclé Province: Holotype male, Parque Nacional General Division Omar Torrijos H., El Cope, $08^{\circ} 49.2^{\prime} 80^{\prime \prime} \mathrm{N}, 80^{\circ} 5^{\prime} 45.7^{\prime \prime} \mathrm{W}, 23-28$ February 2007, collected by hand along hiking trails at night in montane rainforest by V. Townsend, A. Savitzky, and J. Ray (AMNH). Paratypes: 1 subadult male, same location (AMNH); 1 adult male, Carretera El Llano Cartí, Est. Burbayar, Panamá Province (MIUP: no coordinates available); 2 subadult males, 1 subadult female, same location, 9-21 July 2007, R.J. Miranda (MIUP).

Etymology.-The name of this species is based on the Latin words noctis for "night" and scansor for "climber." It is a noun in apposition. This name refers to field observations of behavior in which several individuals (adults and nymphs) were observed climbing tree trunks up to heights of $1-2 \mathrm{~m}$ above the ground after dusk.

Diagnosis.-Large, ventral tubercle on coxa IV located on middle region; rows of subequal tubercles on prolateral and retrolateral surfaces of male femur IV, with retrolateral tubercles slightly larger than prolateral tubercles; femur IV with three distal spiniform tubercles, largest is prolateral,
other tubercles ventral; male tibia IV straight and without 8 12 spiniform tubercles on proximal half; stylus without subdistal pointed apophyses. Superficially, this species resembles Phareicranaus ornatus with respect to scutal outline, dorsal pattern, general penis morphology, and the armature of male femora III-IV. However, Santinezia noctiscansor differs from $P$. ornatus in having a prominent ventral tubercle on male coxae IV (the major character used to distinguish between Phareicranaus and Santinezia). In addition, Santinezia noctiscansor differs from $P$. ornatus with respect to body size, the distribution and relative sizes of spines on the mesal surface of the tibia of the pedipalp, and tarsal formula. With respect to genital morphology, the penis of S. noctiscansor has a ventral plate with 3 distal, curved setae and the glans lacks a dorsal process. In contrast, the penis of $P$. ornatus has 4 distal curved setae and the glans features a dorsal process (Pinto-daRocha \& Kury 2003). Santinezia noctiscansor should be considered a member of the festae group (Pinto-da-Rocha \& Kury 2003) and represents the only known member of this genus that occurs in Panama and Central America. In addition to the position of the large, ventral tubercle on coxa IV in the male, $S$. noctiscansor also shares similar patterns of armature on trochanter III and the femur of the pedipalp with members of the festae group (Pinto-da-Rocha \& Kury 2003). However, in contrast to other species in this group, S. noctiscansor exhibits distinctive morphology with respect to the armature of femur IV of the male. In addition, this species differs from S. arthrocentrica (Mello-Leitão 1943) in the morphology of the stylus and the armature of coxa and tibia IV and differs from S. festae (Roewer 1925) with respect to color pattern and the distribution of tubercles on the carapace.

Description.-Male (holotype): Measurements (mm): Dorsal scutum length 9.32 ; width 10.07 ; cephalothorax length 5.12; width 6.93 ; leg segments (Table 1). Dorsal scutum (Fig. 1): anterior border with a median projection between the chelicerae and a lateral row of 6-7 tubercles on each side.

Eye mound with two large, divergent, spiniform tubercles and two smaller granular tubercles on each side, posterior to the larger tubercles.

Carapace smooth. Lateral margin of scutum with 1-3 tubercles adjacent to area I and 8-9 tubercles adjacent to areas II-III. Area I with a median pair of larger tubercles and one lateral smaller seta-bearing tubercle on each side; area II with transverse row of seta-bearing tubercles; area III with a median pair of large, spiniform tubercles and three smaller seta-bearing tubercles on each side; area IV smooth; posterior border with three lateral seta-bearing tubercles on each side. Free tergite I with two lateral tubercles on each side; II and III with median pair of larger tubercles, with median tubercles on the second free tergite larger than those on the third. Free tergite II with two lateral tubercles on each side; free tergite III with a single lateral tubercle on each side. Anal operculum with several scattered seta-bearing tubercles.


Figures 1-5.-Santinezia noctiscansor, adult male holotype: 1. Habitus, dorsal view; 2. Habitus, ventral view; 3. Habitus, lateral view, arrow indicates position of large, ventral spiniform tubercle on coxa IV; 4. Pedipalpus, left, ventral view; 5. Trochanter-tibia of Leg IV, left, dorsal view. Scale bars $=5 \mathrm{~mm}$.

Venter (Fig. 2): Coxa I with scattered arrangement of four larger tubercles and $8-12$ smaller tubercles; coxa II with median row of six tubercles, two apical tubercles, four anterior tubercles, and 4-5 posterior tubercles; coxa III with median
row of 9-10 tubercles, three anterior tubercles, five posterior tubercles; coxa IV with one stout, larger tubercle covered with many scattered setae near mid-ventral portion (Fig. 3) and an additional $24-30$ scattered smaller tubercles. All coxal


Figures 6, 7.-Santinezia noctiscansor, adult male holotype, penis. 6. Dorsal view, is $=$ inflatable sac of glans, $\mathrm{st}=\mathrm{stylus}, \mathrm{tr}=\mathrm{truncus}, \mathrm{vp}=$ ventral plate; 7. Lateral view. Scale bars $=0.5 \mathrm{~mm}$.
tubercles bear setae. Stigmatic area and free sternites with few, scattered seta-bearing tubercles.

Chelicerae: Basichelicerite with five tubercles; hand with two frontal tubercles; fixed finger with four teeth; moveable finger with four teeth.

Table 1.-Length of the leg segments for adult (holotype) and subadult (paratype from El Cope) males of Santinezia noctiscansor. All measurements are in mm .

| Leg Segment | Leg I | Leg II | Leg III | Leg IV |
| :--- | ---: | ---: | ---: | ---: |
| Adult male |  |  |  |  |
| $\quad$ Trochanter | 1.02 | 1.33 | 1.42 | 2.28 |
| Femur | 6.85 | 14.78 | 11.45 | 16.06 |
| Patella | 1.55 | 2.26 | 2.64 | 3.19 |
| Tibia | 4.05 | 10.57 | 6.51 | 8.40 |
| Metatarsus | 7.95 | 13.35 | 10.81 | 14.89 |
| Tarsus | 3.34 | 8.45 | 5.34 | 6.17 |
| $\quad$ Total length | 24.76 | 50.74 | 38.17 | 50.99 |
| Subadult male |  |  |  |  |
| $\quad$ Trochanter | 0.82 | 1.28 | 1.52 | 2.14 |
| Femur | 6.22 | 13.14 | 10.79 | 13.96 |
| Patella | 1.31 | 1.86 | 2.40 | 2.73 |
| Tibia | 3.71 | 9.44 | 6.04 | 7.80 |
| Metatarsus | 6.92 | 12.16 | 9.81 | 13.61 |
| Tarsus | 2.95 | 7.83 | 4.84 | 5.44 |
| Total length | 21.93 | 45.71 | 35.40 | 45.68 |

Pedipalpus (Fig. 4): Trochanter length: 1.61 mm ; femur length: 4.53 mm ; patella length: 2.03 mm ; tibia length: 3.69 mm ; tarsus length: 4.39 mm ; total length: 16.25 mm . Coxa with one ventral tubercle. Trochanter with two ventral and two dorsal tubercles. Femur with ventral row of seven tubercles, retrolateral row of five tubercles, and dorsal row of seven tubercles (most apical tubercle is larger and spiniform). Patella granular with scattered setae. Tibia dorsally granular, ventrally with four ectal (iIii) and four mesal (IiIi) spines; tarsus dorsally smooth and ventrally with four ectal (IiIi) and four mesal (IiIi) spines.

Legs: Coxae I-II each with one large dorsal tubercle; coxa III smooth; coxa IV with 4-5 latero-dorsal tubercles and one large spiniform apical tubercle. Trochanter I dorsally smooth and ventrally with one prolateral, one median, and 1-2 retrolateral seta-bearing tubercles; trochanter II with one dorsal, three prolateral, one ventral and three retrolateral setabearing tubercles; trochanter III dorsally smooth and ventrally with three prolateral, 3-4 median and three retrolateral setabearing tubercles, apical retrolateral tubercle is largest; trochanter IV dorsally smooth and ventrally with three prolateral, 5-6 median, and three retrolateral seta-bearing tubercles; the apical prolateral and retrolateral tubercles are larger. Femora I-IV granular with organized rows of setae; femora III-IV with prominent tubercles organized into rows with tubercles on femur IV larger than those on III; femur III basally and with one larger dorsal prolateral and one dorsal
retrolateral tubercle and apically with two larger distal retrolateral tubercles; femur IV (Fig. 5) with three larger distal spiniform tubercles on ventral surface, one prolateral and two retrolateral; all three tubercles curved; dorsal row of tubercles with alternating larger and smaller tubercles; tubercles on the retrolateral and prolateral rows largest basally decreasing in size distally. Patellae I-IV granular. Tibiae I-IV granular. Tarsal formula: 9:16:10:11-12, distitarsi I-II with 3 segments.

Male genitalia (Figs. 6, 7): Ventral plate subrectangular, deeply cleft, distal corners without flange. Two groups of setae: two straight latero-basal and three curved latero-apical. Glans without dorsal process, but with inflatable sac with many similar folds arranged in a stack. Stylus smooth, slightly curved. Apex bent, without stylar apophysis.

Color: Body dark reddish brown and legs dark brown to black. Eye mound and median region of carapace lighter brown than rest of carapace. Large yellow spots occur on margin of abdominal scutum adjacent to areas I-III. Median borders of abdominal scutal areas partially outlined by yellow lines (Fig. 1). Median tubercles on areas I-III brown. Posterior borders of free tergites II-III outlined in yellow. Tubercles on second free tergite yellow. Venter dark brown. Chelicerae mottled, darker than eye mound, but lighter than carapace and legs.

Subadult male paratype: Measurements (mm): Dorsal scute length 7.78 ; width 8.82 ; cephalothorax length 4.16 ; width 6.09 ; leg segments (Table 1). Dorsal scutum: same as adult holotype. Venter (Fig. 2): same as adult holotype with the exception that the stout, larger tubercle on the ventral surface of coxa IV is less than half the overall size as that of the adult holotype. Chelicerae: same as adult holotype. Pedipalpus: Trochanter length: 1.28 mm ; femur length: 3.87 mm ; patella length: 1.95 mm ; tibia length: 2.90 mm ; tarsus length: 4.24 mm ; total length: 14.24 mm . Legs: same as adult holotype except tarsal formula: 8:15:9:10. Male genitalia (Figs. 5, 6): same as adult holotype. Color: same as adult holotype.

Distribution.-This species is known from specimens collected from forests in the central Panamanian provinces of Coclé and Panamá, areas west of the Canal Zone.

Habitat.-The adult male holotype and the subadult male paratype from El Coclé were collected from the external surfaces of trunks and moss-covered buttresses of medium to large trees ( $0.5-1.5 \mathrm{~m}$ in diameter) along hiking trails in a moderately sloping montane rainforest. Specimens were collected after dark between $2100-2300 \mathrm{~h}$ during moderate periods of rainfall. No information regarding habitat was available for the MIUP specimens collected from Panamá Province.

Remarks.-During our sampling at the El Coclé field site, we collected adults, subadults, and three other distinct groups of nymphs (based on size and coloration) at the end of February, which corresponds to the early part of the dry season in central Panama. Due to the elevation, the field site was relatively moist and it also rained briefly each evening. The presence of multiple instars in the population indicate that S. noctiscansor is probably sexually active over an extended period of time at this location and that reproduction begins during the later part of the wet season or perhaps earlier. The collection of sexually mature subadults indicates that cranaids
share the novel life history pattern exhibited by other members of the Grassatores, in which there are two instars, the penultimate nymph and adult, in the adult phase (Gnaspini et al. 2004).

The similarities and differences that we observed in the morphology of the subadult and adult male also raise interesting questions concerning the reliability of the identifications of cranaids in regions in which Santinezia species are believed to be syntopic with those of Phareicranaus. The most useful character for distinguishing between these genera is the presence of a prominent ventral tubercle on coxa IV of the male (Pinto-da-Rocha \& Kury 2003). It is our opinion that subadult male Santinezia probably have, at least occasionally, been mistaken for adult male Phareicranaus due to the inconspicuous nature of the ventral tubercle on coxa IV during the penultimate nymph stage.

In comparing the adult male holotype (El Coclé Province) and adult male paratype (Panamá Province), we noticed several asymmetries in the holotype that were not present in the paratype. For example, in the holotype, there is a paracheliceral projection only on the right side of the anterior scutal margin (Fig. 1). In the paratype, this projection is absent and the two sides are symmetrical. Similarly, in the holotype, the left side had a greater number of tubercles than the right with respect to the abdominal scutal areas and the ventral surfaces of the coxae. In the paratype, the tubercles on each side were equivalent in number or differed by only one. The subadult paratypes were also symmetrical with respect to the anterior scutal margin and the distribution of tubercles.

In the field we did not observe any instances of feeding or predation; however, we found that several individuals were parasitized externally by larval mites. In the living condition these mites are orange to red, but when preserved, they quickly turn white (within a few weeks when stored in ethanol). We observed two distinct sizes of these mites on the specimens from El Coclé, which probably represent different species of parasites. Attachment sites for mites included the dorsal scutum, ventral surfaces of coxae and free tergites. The holotype had a small mite attached to the ventral surface of the first coxa, whereas the subadult paratype had two large mites attached to the dorsal scutum near the posterior margin of area III. The intensity of infestation was generally $1-2$ mites per host.

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## LITERATURE CITED

Acosta, L.E., A.P. González \& A.L. Tourinho. 2007. Methods for taxonomic study. Pp. 494-510. In Harvestmen: The Biology of

Opiliones. (R. Pinto-da-Rocha, G. Machado \& G. Giribet, eds.). Harvard University Press, Cambridge, Massaehusetts.
Gnaspini, P., M.B. da Silva \& F.C. Pioker. 2004. The occurrence of two adult instars among Grassatores (Arácnida: Opiliones) - a new type of life cycle in arachnids. Invertebrate Reproduction and Development 45:29-39.
González-Sponga, M.A. 1989. Dos especies nuevas de opiliones del genero Santinezia de Venezuela y redescripcion de Santinezia heliae Avram 1983. Boletin Academia Ciencias Fisicas y Naturales de Caracas 49(155-156):57-77.
Goodnight, C.J. \& M.L. Goodnight. 1947. Studies on the phalangid fauna of Central America. American Museum Novitates 1340:1-21.
Kästner, A. 1937. Chelicerata 7. Ordnung der Arachnida: Opiliones Sundeval Weberknechte. Pp. 300-393. In Handbuch der Zoologie. Volume 3, Number 2. (W. Kukenthal \& T. Krumbach, eds.). Walter de Gruyter \& Co., Berlin \& Leipzig.
Kury, A.B. 2003. Annotated catalogue of the Laniatores of the New World (Arachnida, Opiliones). Revista Ibérica de Aracnología 31:1-337.
Machado, G. \& J. Warfel. 2006. First case of maternal care in the family Cranaidae (Opiliones, Laniatores). Journal of Arachnology 34:269-272.
Mello-Leitão, C.F de. 1926. Notas sobre Opiliones Laniatores sulamericanos. Revista do Museu Paulista 14:327-383.
Mello-Leitão, C.F. de. 1932. Opiliões do Brasil. Revista do Museu Paulista 17:1-505.
Mello-Leitão, C.F. de. 1935. Algumas notas sobre os Laniatores. Archos Museu do Nacional Rio de Janeiro 36:87-116.
Mello-Leitão, C.F. de. 1943. Arácnidos recogidos en el Ecuador y en el Perú por la señora H. E. Frizell Don. Comunicaciones Zoologicas Museo Historia Natural Montevideo 5:1-8.
Pinto-da-Rocha, R. \& A.B. Kury. 2003. Phylogenetic analysis of Santinezia with description of five new species (Opiliones, Laniatores, Cranaidae). Journal of Arachnology 31:173-208.
Pinto-da-Rocha, R. \& A.B. Kury. 2007. Cranaidae. Pp. 185-188. In Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G.

Machado \& G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.
Roewer, C.F. 1913. Die Familie der Gonyleptiden der OpilionesLaniatores. Archiv für Naturgeschichte, Berlin, Abteilung A:257-473.
Roewer, C.F. 1923. Die Weberknechte der Erde. Systematische Bearbeitung der bisher bekannten Opiliones. Gustav Fischer, Jena.
Roewer, C.F. 1925. Opilioniden aus Süd-Amerika. Bolletino dei Musei di Zoologia ed Anatomia Comparata della Universita di Torino, NS 34:1-34.
Roewer, C.F. 1932. Weitere Weberknechte VII. (7. Ergänzung der Weberknechte der Erde, 1923). Archiv für Naturgeschichte, Berlin 1:275-350.
Roewer, C.F. 1943. Weitere Weberknechte XI: Über Gonyleptiden. Senckenbergiana 26:12-68.
Roewer, C.F. 1963. Opiliones aus Peru und Colombia (Arachnida Arthrogastra aus Peru V). Senckenbergiana Biologica 44:45-72.
Soares, B.A.M. \& H.E.M. Soares. 1948. Monografia dos gêneros de opiliões neotrópicos I. Arquivos de Zoologia do Estado de São Paulo 5:553-636.
Soares, H.E.M. 1970. Novas espécies de opiliões da Região Amazônica (Opiliones, Cosmetidae, Gonyleptidae, Phalangiidae, Stygnidae). Revista Brasileira Biologia 30:323-338.
Townsend, V.R. Jr., D.N. Proud \& M.K. Moore. 2008a. Harvestmen (Opiliones) of Trinidad, West Indies. Living World 2008:53-65.
Townsend, V.R. Jr., D.N. Proud, M.K. Moore, J.A. Tibbetts, J.A. Burns, R.K. Hunter, S.R. Lazarowitz \& B.E. Felgenhauer. 2008b. Parasitic and phoretic mites associated with neotropical harvestmen from Trinidad, W. I. Annals of the Entomological Society of America 101:1026-1032.
Townsend, V.R. Jr., N.J. Rana, D.N. Proud, M.K. Moore, P. Rock \& B.E. Felgenhauer. 2009. Morphological changes during postembryonic development in two species of Neotropical harvestmen (Opiliones, Laniatores, Cranaidae). Journal of Morphology 270:1055-1068.

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